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Spatial Context And The Role Of Competition In Oviposition Habitat Selection By Cope'S Grey Treefrog (Hyla Chrysoscelis) And Culex Restuans Mosquitoes

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SPATIAL CONTEXT AND THE ROLE OF COMPETITION IN OVIPOSITION HABITAT SELECTION BY COPE'S GREY TREEFROG (*HYLA CHRYSOSCELIS*) AND *CULEX RESTUANS* MOSQUITOES

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ABSTRACT

The Ideal Free Distribution (IFD) is an influential ecological model for predicting distribution of populations. Since its inception, attempts have been made to improve the IFD, including addition of spatial context. Spatial contagion is a newer ecological concept wherein quality of a habitat patch may affect the perception of neighboring patches. Using Cope's gray treefrog (*Hyla chrysoscelis*) and *Culex* mosquitoes (*Culex restuans*), I conducted a series of outdoor mesocosm experiments to test key predictions of the IFD and address how it interacts with spatial contagion effects. I found some support for the IFD prediction that individual *H. chrysoscelis* should avoid habitat patches with higher densities of conspecifics although there was not a clear linear relationship, as would be expected. There was a strong effect of distance from the nearest tree line on oviposition habitat selection and an interaction between distance and conspecific density. It is possible that the costs of movement by ovipositing *H. chrysoscelis* females may outweigh the potential costs of intraspecific competition, which would violate the IFD assumption that individuals are free. Conversely, a second experiment using *H. chrysoscelis* revealed that the presence of conspecifics can affect the hierarchy of habitat patches by causing females to avoid larger pools that have been previously described as optimal. My results suggest that individuals are capable of distinguishing patches based upon conspecific densities, but the relationship may be a binary threshold rather than a linear relationship. Using *C. restuans*, I found that while females avoided patches containing conspecifics, resource availability was a more significant predictor of where egg rafts were laid. Resource availability did not have a

reward contagion. While competition does play a role in habitat selection, these results suggest that other environmental factors may be more crucial in habitat selection.

ACKNOWLEDGEMENTS

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CHAPTER I: THE IDEAL FREE DISTRIBUTION IN COPE'S GRAY TREE FROG (*HYLA CHRYSOSCELIS)*

Introduction

Understanding the decision making process that underlies habitat selection is imperative to improving both ecological modelling and habitat management. Habitat selection is the process by which individuals actively choose habitat patches based on perceived patch quality (Fretwell and Lucas 1970). Historically, ecological community composition emphasized post-colonization effects, such as species sorting and environmental filtering, with little emphasis on habitat selection (Brown and Swan 2010, Heino et al. 2015, Cadotte and Tucker 2017). However, recent research has shown that habitat selection can have important ecological and evolutionary consequences, as it can lead to increases in local adaptation, genetic variation, population genetic structure, and reproductive isolation (Nicolaus and Edelaar 2017). Understanding the how animals select habitat is of interest to conservation biologists, wildlife managers, and evolutionary biologists because this process can impact species distributions, fitness, and speciation (Fretwell and Lucas 1970, DeMeeus et al. 1993). With such an expansive impact on the natural world, habitat selection clearly warrants continued, intensive study.

Many theories and models of habitat selection stem from the Ideal Free Distribution model, hereafter referred to as the IFD (Fretwell 1972, Fagen 1987, Goss-Custard et al. 1995). This model proposes that individuals within a population distribute themselves among available patches based on habitat quality (Fretwell and Lucas 1970). The model assumes that individuals are ideal or have perfect information about all available habitat patches they encounter, and thus

should select the highest quality habitat patch to maximize their fitness. This part of the IFD makes it an evolutionarily stable model, as those individuals who have perfect information about the available habitat patches will be selected for (Cantrell and Cosner 2018). There are a number of studies that directly or indirectly support this first assumption of the IFD (Harper 1982, Godin and Keenleyside 1984, Sutherland et al. 2016). However, some research on the IFD has misinterpreted the influence of resource distribution by assuming the input of resources is continuous when it is not (Tregenza 1994). Additionally, meta-analysis done by Kennedy and Gray (1993) found that the distribution of individuals was consistently less extreme than the resource distribution, suggesting that while individuals can assess resource availability, they tend to under-use high quality sites and over-use low quality sites, which suggests a violation of this first assumption of the IFD.

A second assumption of the IFD is that habitat patches are equally accessible and that individuals are free to enter any habitat patch. Hence, individuals are equally likely to inhabit any given patch, all things being equal. However, individuals do vary in their ability to assess and enter a given habitat. Additionally, movement between patches has an inherent cost in terms of energy used to move from one patch to another, and all patches may not be equally accessible, as movement to distant patches will incur higher costs. Finally, it is unlikely that late-arriving colonists will experience the same conditions as current patch residents, due to territoriality and decreases in perceived quality (Fretwell 1972).

When resources are limited, presence of competitors should be a significant factor in individual habitat choice. For example, female mosquitoes, *Culiseta longiareolata*, oviposited more in water that contained a lower density of conspecific larvae (Kiflawi et al. 2003). The IFD predicts that each patch within a system should have a baseline quality, but as density of

conspecifics increases, quality should decrease (Fig. 1.1). Ecological systems are complex, and there are often multiple factors that can affect habitat quality. For aquatic systems, this can include factors such as predation, resource availability, water conductivity, and pond age (Werner and Hall 1988, Klaver et al. 2013, Pintar and Resetarits 2017). In more complex settings where multiple habitat patches with different baseline qualities are present, the presence of competition will change individual site quality, as well as how neighboring patches are perceived. For example, in Figure 1.2, patch one has the highest baseline quality (shown by B1) and as individuals begin to colonize the system, the IFD predicts that they should colonize patch one first. As colonization continues, quality (P1) decreases until it is on par with the baseline quality of patch two. Once this occurs, patch one and patch two should be colonized at equal rates. Their quality will continue to decline until they are both on par with patch three, at which point all three patches will be colonized equally.

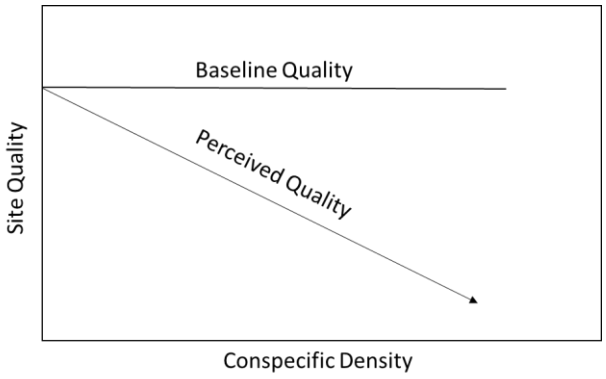

Figure 1.1. Baseline quality represents site quality when density = 0. As population density increases, the perceived quality of a habitat decreases.

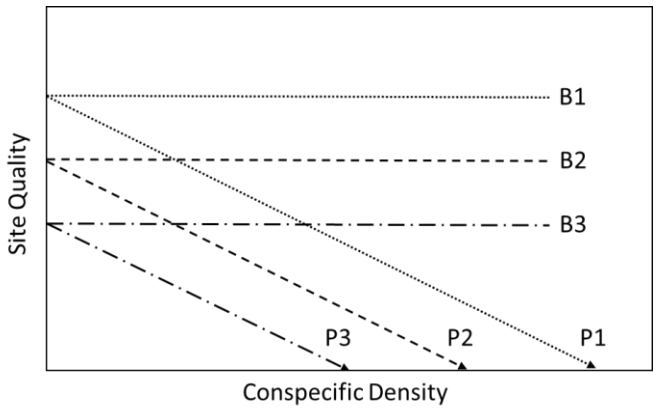

Figure 1.2. Habitat quality vs. density of three theoretical habitat patches. Patch 1 has the highest base quality (B1) and is the first to be colonized. As density increases, the perceived quality of Patch 1 (P1) decreases until it is equal to the base quality of Patch 2 (B2). At this point density of Patch 1 and Patch 2 grow proportionally such that P1 = P2. As the densities in Patch 1 and Patch 2 increase, the quality of each patch continues to decrease until P1 and P2 are equal to the base quality of Patch 3 (B3). After this, the density of all three patches would grow proportionally such that P1 = P2 = P3.

Here, I present two studies to test major predictions of the IFD and better understand factors influencing oviposition habitat selection. Both were outdoor mesocosm experiments that were designed to test the oviposition habitat selection of *H. chrysoscelis.* The first experiment focused on the IFD prediction that individuals should choose a habitat patch where intraspecific competition is lowest, and I tested this by using mesocosms containing five different densities of conspecific larvae. The second experiment tested the IFD prediction that the first patch colonized should have the highest quality, but that as conspecific density increases new colonizers should prefer other patches with lower base qualities. This was done by crossing conspecific larval density with pool size. Female *H. chrysoscelis* are known to prefer ovipositing in larger pools (Resetarits et al. 2018). Females should oviposit in large pools with lower larval densities, but if larval density increases to a certain threshold within large pools, females should show a linear shift towards ovipositing in smaller, larvae-free pools.

Methods

Study Site

All studies were completed at the University of Mississippi Field Station (UMFS) in Lafayette County, Mississippi. The UMFS covers 318 hectares and contains over 200 ponds along with a variety of streams, wetlands, fields, forests, and a wide variety of wildlife.

Study organism

Cope's Grey Tree frog, *Hyla chrysoscelis. H. chrysoscelis* breeds from mid-April to mid-August (Ritke et al. 1990), and is the only anuran known to readily oviposit in experimental pools at the UMFS. *H. chrysoscelis* lay their eggs in large, floating packets that are relatively easy to collect and quantify.

Experiment 1: Does conspecific density affect oviposition habitat selection?

The IFD prediction that the presence of competitors should negatively affect perceived habitat quality was tested using an outdoor mesocosm experiment. Nine experimental blocks were set up, each containing five 1200 L cattle tanks (Fig. 1.3). Within a block, each tank contained a different density of *H. chrysoscelis* larvae: 0 (control), 75, 150, 300, or 600. Tanks within a block were five meters apart from adjacent tanks and were situated in a pentagon to be equidistant from a central point (Fig. 1.3). Blocks were set up a minimum of 10 meters apart so that colonizing individuals would assess them as separate localities (Resetarits et al. 2018). Additionally, once each block was set up, the distance of each tank from the nearest tree line was measured. This experiment began on 4 April 2019. Due to logistical constraints, only three blocks could be set up at a time. Additionally, experimental blocks were taken down after three weeks in order to avoid the loss of larvae due to metamorphosis (Wilbur and Alford 1985). Thus

blocks 1–3 ran from 28 May – 18 June, blocks 4–6 ran from 28 June – 19 July, and blocks 7–9 ran from 31 July – 21 August.

Prior to establishing each set of blocks, *H. chrysoscelis* eggs were collected and reared to the 17th – 20th Gosner stage (Gosner 1960). Tanks were filled with well water, received 2.2 kg of leaf litter, and were covered with 1.13 x1.3 mm mesh screens to prevent colonization until the experiment began. Once blocks were physically set up and larvae were ready, treatments were randomly assigned to each tank. The designated number of larvae was then added to each tank along with 2 L of pond inoculum (water collected from nearby, predator-free ponds). After everything was added, the screens covering tanks were partially sunk to allow for colonization.

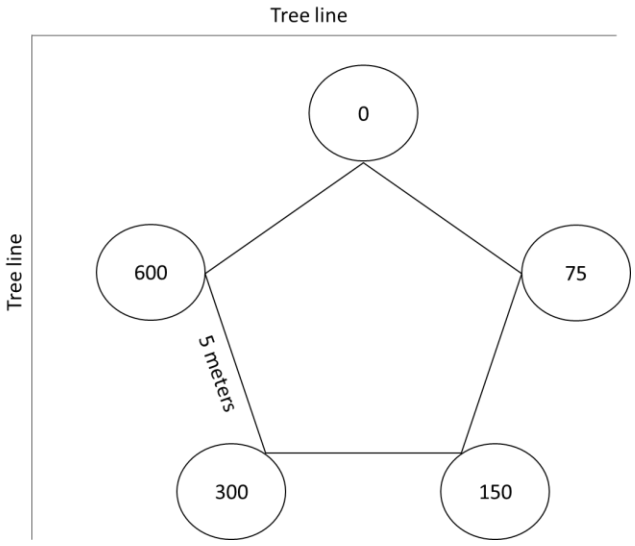

Figure 1.3. Schematic of design for a block of Experiment 1. Pools were placed in a pentagon and set 5 meters apart from adjacent pools. Pools were then randomly assigned a larval density of 0, 75, 150, 300, or 600.

Data collection began on 28 May. For three weeks, Tanks were checked daily for *H. chrysoscelis* eggs, which were collected and taken to the lab to be photographed and counted using ImageJ (Schneider et al. 2012, Bohenek and Resetarits 2017). .

After three weeks, all pools within a set of block were drained and cleaned, and a new set of blocks was set up using the methods described above. For blocks 1–3, tadpoles were released into nearby ponds. Due to concerns about differing larval survival rates among treatments, I collected and counted all leftover tadpoles in blocks 4–9 to quantify survival. However, I found no significant affect of density on larval survival rates, so this is not discussed further.

Variation in oviposition was tested with linear mixed-effects models using treatment and distance from tree line as predictors and block as a random factor. Before these models were constructed, I conducted a linear regression of distance from tree line and the mean number of eggs per tank. I constructed four different models testing the following response variables: 1) mean number of eggs per tank; 2) mean number of hits per active block night; 3) mean number of eggs per active block night; and 4) mean number of eggs per hit. A hit is defined as any night when a tank received eggs, and an active block night is anytime that a block received eggs. Thus, hits per active block night is the proportion of activity within a tank compared to all activity within a block. Mean number of eggs per active block night was calculated by dividing the total number of eggs deposited in a tank by the number of nights with oviposition events in a block. For the final response, the total number of eggs deposited in a tank was divided by the number of hits that tank had. All response variables were normally distributed and did not require transformation. Once constructed, all models were then tested using Type III analysis with Satterthwaite's method (Bates et al. 2015, Kuznetsova et al. 2017).

In addition to creating linear mixed-effects models, a one-way Dunnett's procedure was to compare all treatments to the control, predicting that responses would be lower in treatments than the control. A linear regression was used to determine the effect of distance from tree line alone on oviposition. All analyses for this experiment were done using R v.3.5.2 (R Core Team

2019). All linear mixed models were constructed using the lme4 package and tested using the lmerTest package (Bates et al. 2015, Kuznetsova et al. 2017). Dunnett's procedure used the multcomp package (Hothorn et al. 2008).

Experiment 2: Does conspecific density alter perceived habitat quality?

This experiment tested another major prediction of the IFD about the order in which patches should be colonized. In any system, the first patch to be colonized should be the patch with the highest base quality (patch size), but as conspecific density in that patch increases new individuals should start to prefer other patches with a lower base quality. This prediction was tested using an outdoor mesocosm experiment. Six blocks were set up, each containing three tanks, two 1.13 m^2 (small) and one 5.73 m^2 (large) tank (Fig. 1.4). Previous research has shown that ovipositing *H. chrysoscelis* prefer to oviposit in larger pools (Resetarits et al. 2018), so, in order to simulate the IFD, larvae were added to the larger tanks. Two small tanks were added to each block because one small tank could quickly become oversaturated with eggs, which could lead to females ovipositing even more in large tanks and potentially skewing any effect of competition. Additionally, this experiment utilized two different densities of larvae: 600 or 1200. These numbers were based on previously observed densities of larvae in large tanks. Two different densities were used to test whether there was a linear response to conspecific larvae. It is possible that at lower densities the larger tanks would still be viewed as optimal. In order to test for this and test whether higher densities of conspecifics can cause habitat preference to change, two densities had to be used: one below and one above that critical threshold. The densities chosen for this experiment were based on previously observed, naturally established, larval densities within experimental mesocosms (Resetarits, *unpublished data*).

Set up for this experiment began on 28 April 2019. Blocks were set up 5 m from the tree line and ≥ 10 m from other all other experimental blocks. Within each block, tanks were set up in a triangle, with one pool closest to the forest edge (Fig. 1.4). All pools were filled with well water to a depth of 0.5 m and as a result small pools held 593 L, and large pools held 3,002 L (Resetarits et al. 2018). For leaf litter, 0.9 kg with 1 L of pond inoculum were added to small pools, and 4.4 kg and 4 L of pond inoculum were added to large pools. This was done to establish micro-organism communities in tanks similar to those found in natural ponds at the UMFS. Pools were then covered with 1.13 x 1.3 mm mesh screens to prevent colonization. *H. chrysoscelis* eggs were collected prior to the beginning of this experiment and reared to Gosner stages17–20 (Gosner 1960). Finally, I assigned larval treatments to each tank (0 for small tanks, 600 or 1200 for large tanks), and added larvae. Once the larvae were added, screens were partially sunk to open tanks to colonization, and the experiment began.

Twelve blocks were set up for this experiment. Due to issues of space, only six blocks could be set up at one time. As with the first experiment, all blocks were taken down after three week in order to avoid loss of larvae due to metamorphosis (Wilbur and Alford 1985). As such, blocks 1–6 ran from 25 May – 15 June and blocks 7–12 ran from 20 June – 11 July. When blocks 1–6 were complete, all tanks were drained and cleaned, and remaining larvae were released to nearby ponds. Once tanks were cleaned, they were set up again using the methods described above, for blocks 7–12. This experiment was terminated on 11 July 2019.

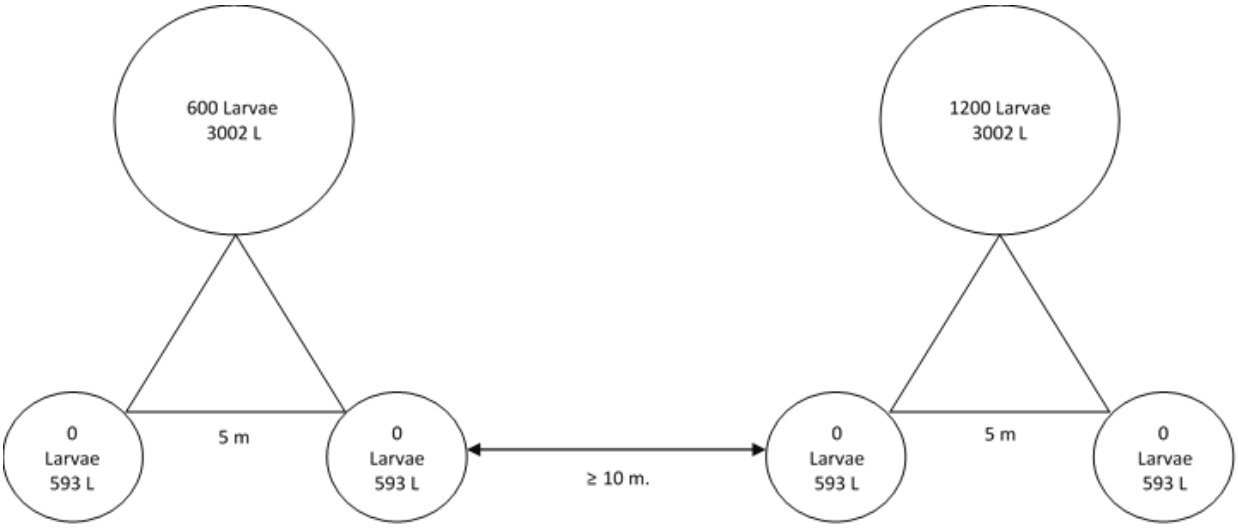

Figure 1.4. Each block consisted of three pools: One large (3002 L) pool and two small (593 L) pools. Large pools were filled with either 600 or 1200 *H. chrysoscelis* larvae. Pools within a block were placed 5 m apart. Blocks were a minimum of 10 m apart.

Because there were more small tanks than large, directly comparing responses would not give an accurate depiction of oviposition habitat selection. Instead, for all response variables the means of small and large tanks from each block were compared. The number of eggs laid was measured using three different metrics: 1) the mean number of eggs laid in each tank; 2) the total number of eggs laid in each tank scaled by the size of the tank (total number of eggs /conversion factor), 3) the proportion of eggs laid in a tank from all eggs laid in a block (total number of eggs in tank / total number of eggs in block). The number of eggs scaled by tank size allowed for a more direct comparison of large and small tanks. For this measurement, scaling was relative to small tanks; large tanks are 5.06x the size of small tanks, so to scale oviposition the total number of eggs in large tanks was divided by 5.06 while the number of eggs in small tanks was divided by 1. Both the scaled and proportional number of eggs laid per pool were square root transformed to be normally distributed. Three linear mixed-effects models were conducted treating total number of eggs, scaled number of eggs, or proportion of eggs as the response

variable and tank size and number of larvae in large pools as the categorical predictors with block as a random factor.

Two other measures of response included the number of hits per active block night and the mean number of eggs deposited per active block night as a function of pool size and larval density. To analyze hits per active block night, I compared the number of nights that a pool had eggs laid in it to all active block nights, which is defined as any night when a block received eggs. Hits per active block night was square root transformed to meet the assumption of normality. The number of eggs deposited per active block night was measured by dividing the total number of eggs laid in a pool by the number of active block nights for that pool. Analysis for both hits per active block night and mean eggs per active block night was done using a linear mixed-effects model with tank size and larval density as predictors and block as a random factor. All models for this experiment were tested using Type III analysis with Satterthwaite's method. All analyses were done using R v.3.5.2, and linear mixed-effects models used the lme4 package as well as the lmerTest package (Bates et al. 2015, Kuznetsova et al. 2017, R Core Team 2019).

Results

Experiment 1:

Linear regression showed a significant negative effect of distance on the mean number of eggs deposited per tank ($t = -3.76$, $P < 0.001$) (Fig. 1.6). Additionally, in all four linear mixed-effects models, there was a significant negative effect of distance from tree line on the probability of oviposition (see Table 1.1). There was a significant effect of larval density on oviposition in the model of hits per active block night ($F_{4,33} = 3.77$, $P = 0.01$), eggs per active block night ($F_{4,34} = 5.00$, $P = 0.002$), and mean eggs per hit ($F_{4,34} = 3.36$, $P = 0.02$). Larval

density had a marginal effect on the mean number of eggs per tank ($F_{4,35} = 2.26$, P = 0.08). Dunnett's procedure showed a significant difference between the 0 larvae control and 300 larvae treatment for the mean number of eggs per tank (Z = -2.756, P = 0.01), hits per active block night (Z = -3.329, P = 0.002), eggs per active block night (Z = -3.546, P < 0.001), and mean eggs per hit (Z = -2.957, P = 0.006)(Table 1.2). There was a significant interaction between distance and treatment when the number of hits per active block night ($F_{4,33} = 3.02$, P = 0.03, Fig. 1.5b) or eggs per active block night ($F_{4,34} = 3.66$, P = 0.01, Fig. 1.5c) were measured. A linear mixed model of the mean number of eggs per hit showed a marginal effect of the interaction between treatment and distance ($F_{4,35} = 2.49$, P = 0.06, Fig. 1.7d). There was no interaction when measuring mean number of eggs ($F_{4,35} = 1.08$, P = 0.38, Fig. 1.5a).

Table 1.1 Results for linear mixed models testing the effects of density and distance on the mean number of eggs laid per pool (Mean), hits per active block night (HPABN) eggs per active block night (EPABN) and mean eggs per hit (MEPH). Table also shows the interaction between distance and density. Significant effects are in bold, marginal effects are in italics.

	Density				Distance			
	NumDF	DenDF	F value	P value	NumDF	DenDF	F value	P value
Mean	4	34.77	2.435	*0.065*	1	33.56	11.281	**0.002**
HPABN	4	32.71	3.724	**0.013**	1	29.58	13.125	**0.001**
EPABN	4	33.78	4.635	**0.004**	1	30.65	11.877	**0.001**
MEPH	4	33.48	3.356	**0.02**	1	30.97	9.647	**0.004**

	Distance x Density			
	NumDF	DenDF	F value	P value
Mean	4	34.85	1.17	0.341
HPABN	4	33.11	2.991	**0.033**
EPABN	4	33.64	3.359	**0.02**
MEPH	4	33.84	2.493	*0.061*

Table 1.2. Standard deviation, standard error, Z values, and P values for one-way Dunnett's procedure comparing the 300 larvae treatment to the control (0 larvae) for each response

variable, predicting that densities higher than 0 would receive less eggs. Significant values are in bold.

	Estimate	Error	Z value	P value
Mean	-7427	2543	-2.921	**0.007**
HPABN	-1.25	0.377	-3.309	**0.002**
EPABN	-1493.91	435.09	-3.434	**0.001**
MEPH	-2214	750.2	-2.951	**0.006**

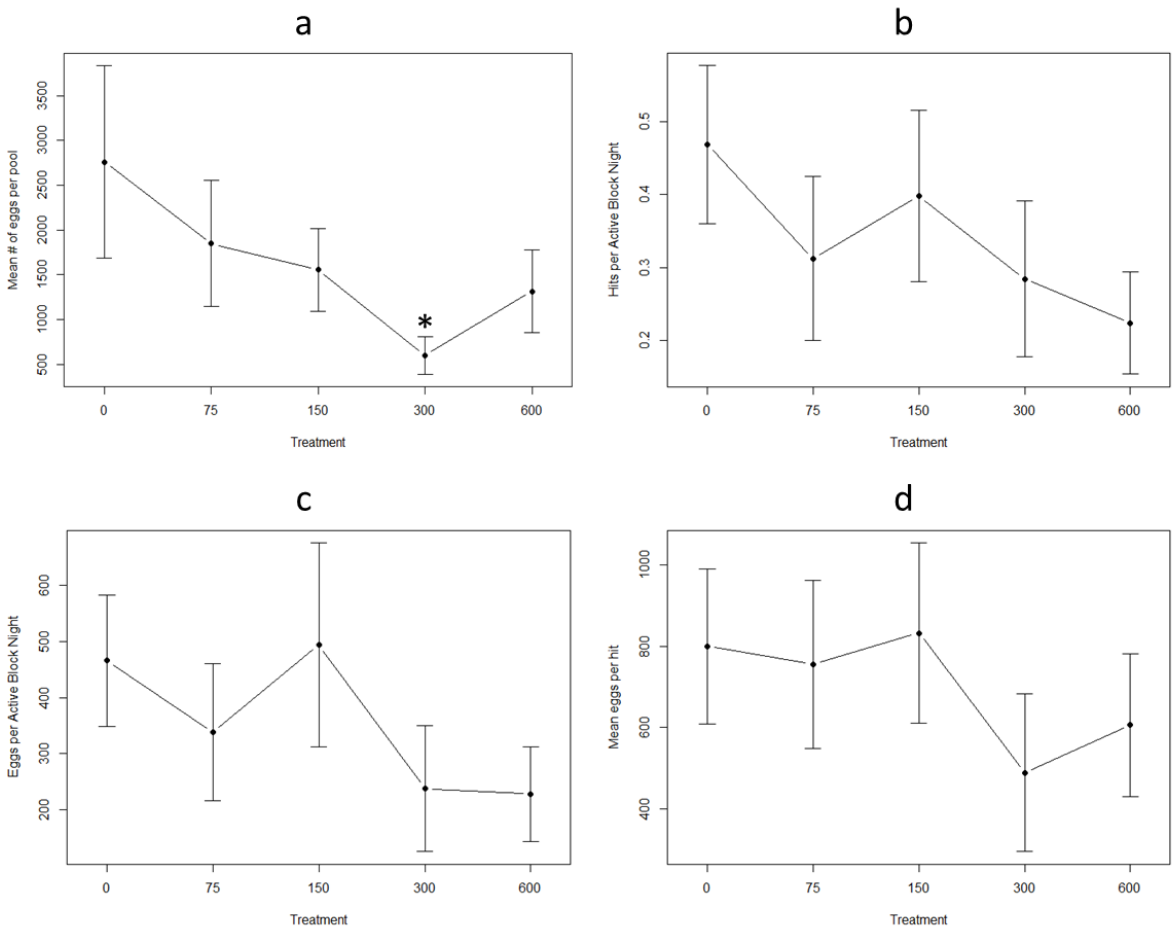

Figure 1.5. The effect of larval density on (a) total number of eggs per pool, (b) hits per active block night, (c) eggs per active block night, and (d) mean eggs per hit. Significant differences from control are indicated by asterisk.

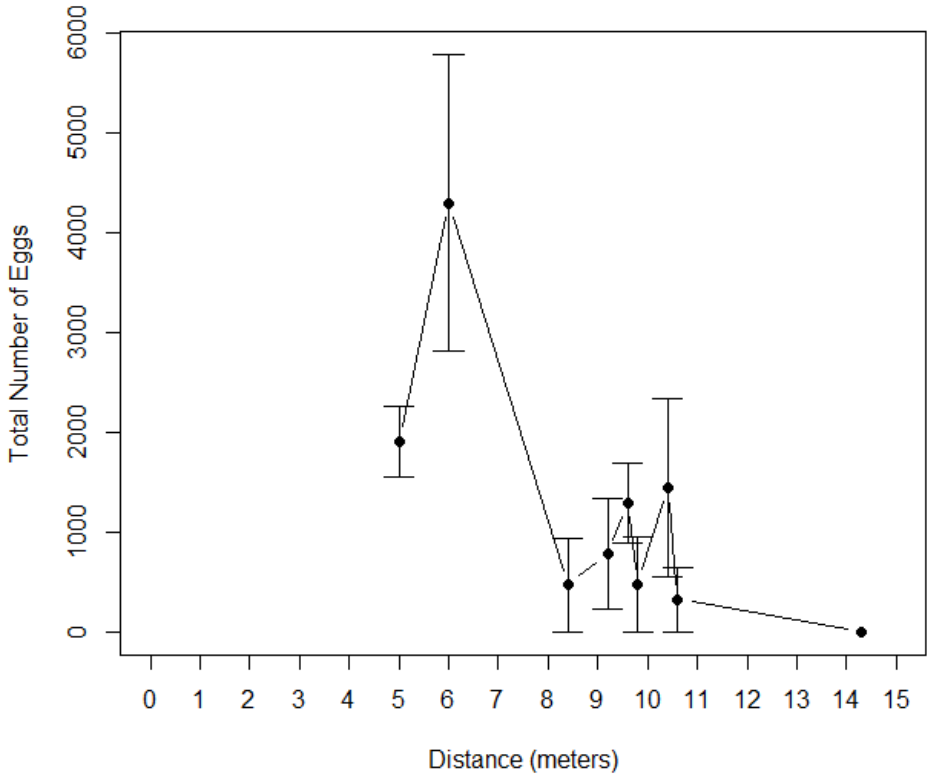

Figure 1.6. The effect of distance from tree line on egg deposition.

Experiment 2:

Tank size had a significant effect on the mean number of eggs deposited in each pool ($F_{1,10}$ = 17.47, P = 0.002, Fig. 7a). Density of larvae did not have an impact on the total number of eggs deposited ($F_{1,10}$ = 0.1469, P = 0.71), and there was no significant interaction between size and larval density ($F_{1,10}$ = 0.0001, P = 0.99, Fig. 1.8a). When the number of eggs deposited was scaled based on size of tank, there was no significant difference based on tank size ($F_{1,10}$ = 2.56, P = 0.14) or larval density ($F_{1,10}$ = 0.4303, P = 0.5267), and there was no significant interaction between pool size and larval density ($F_{1,10}$ = 0.1583, P = 0.70, Fig. 1.8b). For the proportion of egg laid per pool there was a significant effect of pool size ($F_{1,20}$ = 72.35, P < 0.01) but not larval

density ($F_{1,20}$ = 0.05, P = 0.81), and there was no interaction between pool size and larval density ($F_{1,20}$ = 0.06, P = 0.79, Fig. 1.8c). Analysis for the mean number of eggs, scaled number of eggs, and proportion of total eggs from block are summarized in Table 1.3.

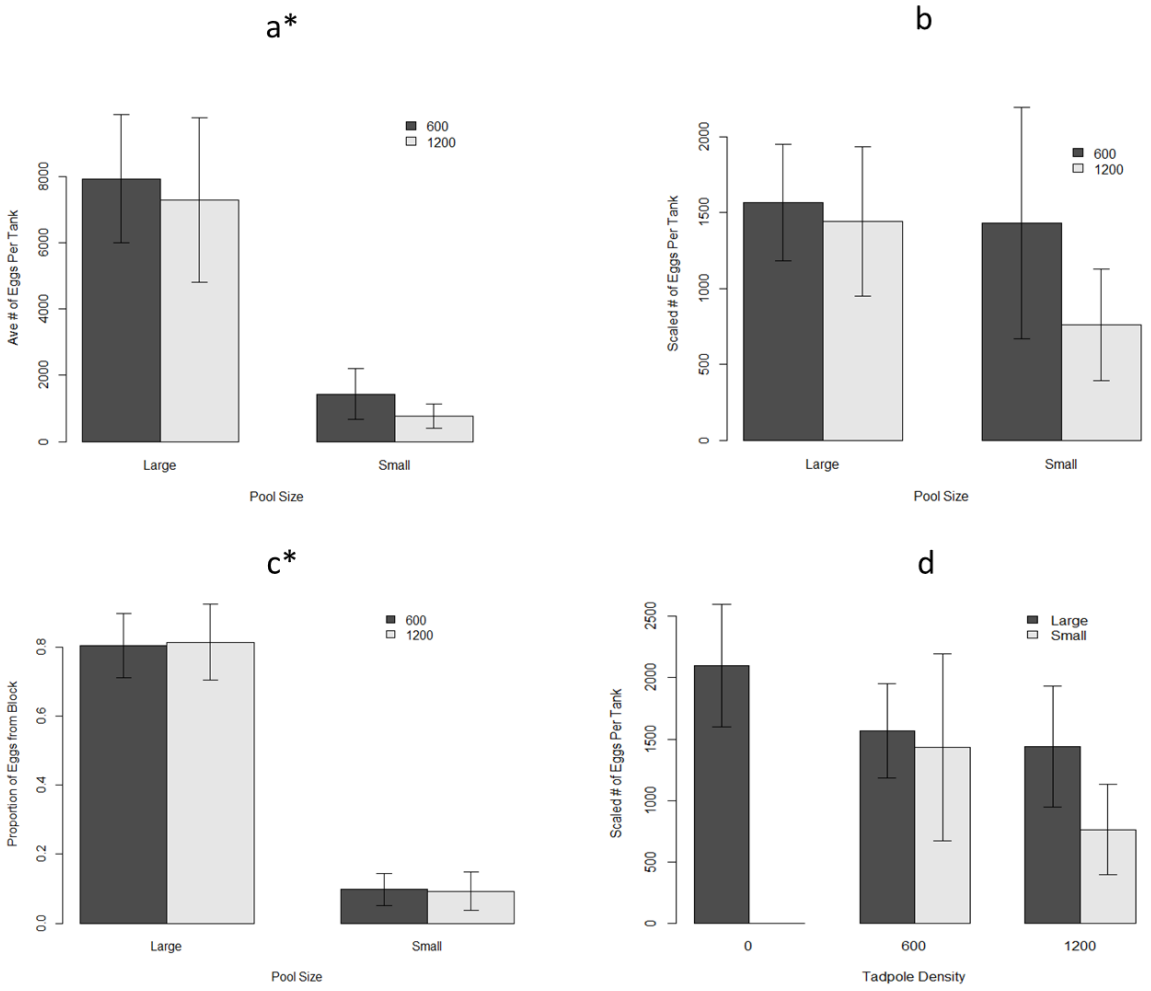

Figure 1.7. (a) Mean number of eggs deposited per pool as a function of pool size and larval density. (b) The number of eggs laid in pool normalized by size. (c) The proportion of eggs laid in a pool from all eggs laid in a block. * Indicates that there was a significant difference between pool sizes. (d) Comparison of scaled number of eggs in 600 and 1200 treatments to results of Resetarits et al (2018) (0 Larvae).

Table 1.3 Summary of results of linear mixed effects model of the mean number of eggs per pool, normalized number of eggs per pool, and proportion of eggs in each pool from block. Table shows F and P values for the effect of size and larvae along with the interaction between size and larvae. Significant effects are in bold.

	Size		Larvae		Size x Larvae	
	F value	P value	F value	P value	F value	P value
Mean	17.4723	**0.0019**	0.1469	0.7095	0.0001	0.9919
Scaled	2.5589	0.1408	0.4303	0.5267	0.1583	0.6991
Proportion	72.3466	**>0.001**	0.0588	0.8109	0.0671	0.7983

There was a significant effect of pool size ($F_{1,20} = 69.93$, $P < 0.001$) but not larval density ($F_{1,20} = 0.007$, $P = 0.98$) or a significant interaction between size and larval density ($F_{1,20} = 0.04$, $P = 0.85$) on the number of hits per active block night (Fig. 1.9a). For the mean number of eggs deposited per active block night, there was a significant effect of size ($F_{1,10} = 26.88$, $P < 0.001$); however there was no significant effect larval density on mean eggs per hit ($F_{1,10} = 0.49$, $p = 0.49$) or significant interaction of size and larval density ($F_{1,10} = 1.37$, $P = 0.26$) (Fig 1.9b).

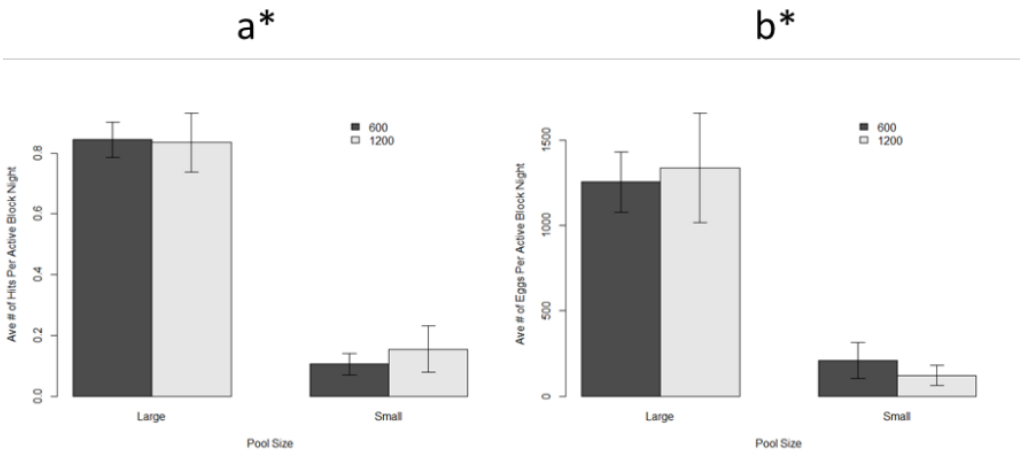

Figure 1.8. (a) Mean number of oviposition events (hits) per active block night. (b) Mean number of eggs laid per active block night. * Indicates that there was a significant difference between pool sizes.

Table 1.4. Summary of the ANOVA testing the effects of size and larvae on number of hits per active block night (HPABN) and eggs per active block night (EPABN). Analysis also includes the interaction between size and larvae. Significant effects are represented in bold.

	Size		Larvae		Size x Larvae	
	F value	P value	F value	P value	F value	P value
HPABN	69.931	**5.84e-08**	0.001	0.979	0.037	0.850
EPABN	34.261	**1e-05**	0.000	0.986	0.188	0.669

Discussion

These results provide some evidence that density of conspecifics negatively impacts perceived habitat quality, consistent with the predictions of the IFD. For example, there was a significant difference between the control and 300 larvae treatments suggesting that female *H. chrysoscelis* can differentiate habitat patches based on conspecific density. However, the fact that no other larval density was differentiated from the control suggests that their decision making is not perfect. The significant effect of distance from the tree line on oviposition was an unexpected effect of the experimental design. The fact that larval density had a significant effect when distance from tree line was used as a covariate suggests that distance interfered with the effect of conspecific larvae. The effect of distance and interaction constitute a clear violation of the IFD's second assumption. However, while there was a clear interaction between distance and treatment, the meaning and ecological relevance of this interaction was unclear.

The fact that distance interacted significantly with treatment could be interpreted as interference. This, combined with the significant difference found between the control and 300

larval density treatment, suggests that there may be a weak effect of conspecific density on oviposition habitat selection, but that the effect of conspecifics is countered by the distance from tree line. There are a variety of potential explanations as to why distance had an effect in this experiment. One potential explanation for the effect of distance is the energy costs for *H. chrysoscelis* to travel from tree canopy to breeding sites. Females travel from the forest to find males calling from the edge of temporary ponds (Bertram et al. 1996). Once females find the calling males they initiate amplexus and can choose an oviposition site (Resetarits and Wilbur 1991). However, travel to find a mate and suitable breeding habitat could incurs a significant energetic cost. Additionally there may be other factors, unrelated to energy costs. Moving between habitat patches can involve significant risks such as predation. Additionally, the perceived effect of distance may not have actually been distance, but instead order in which patches are encountered. In this case, the patches closer to the tree line were more likely to be encountered and thus more likely to be oviposited in.

I found strong evidence for another key prediction of the Ideal Free Distribution, that high quality patches should receive the highest initial colonization, but colonization should decrease as conspecific density increases. While there was a strong effect of tank size on the mean number of eggs deposited, when the number of eggs was scaled to tank size there was no significant difference between large tanks, which contained larvae, and small tanks, which did not. This means that the difference seen in egg deposition in this experiment was may not have been a result of non-random habitat selection by *H. chrysoscelis*, but could simply be a result of larger patches being larger targets, via the target-area effect. (Simberloff 1974). This is in opposition to previous research, which has shown that *H. chrysoscelis* prefer to oviposit in larger pools, even when scaled for size (Resetarits et al. 2018). This suggests that females respond to

larvae presence or absence, but do not differentiate among pools with different larval densities. Based on the results of these two experiments, oviposition by *H. chrysoscelis* matches the prediction of the IFD that competition affects habitat selection. However, both experiments suggest a threshold effect instead of linear response to conspecific density, which violates the IFD's first assumption.

The results of these experiments and previous research raise two major questions. The first is why females prefer larger pools. A likely possibility could be that larger pools have more resources and a lower risk of desiccation. However, in this experiment, I normalized the amount of resources relative to pool size. Additionally, previous research has shown that hydroperiod is reliant on factors other than pond size such as vegetation and underlying hydrology (Eason, Jr and Fauth 2001). With this in mind, it remains to be understood why females would show a preference for pond size and may warrant further study.

The second question raised relates to the perplexing effect of competition. Previous research in *H. chrysoscelis* and other anuran species has shown a strong, negative effect of conspecific density on development of larvae (Morin 1986, Stein and Blaustein 2015, Crossland et al. 2019). Females should show a strong, negative, linear response in oviposition habitat selection to ponds containing higher proportions of conspecific larvae. However, when tested alone, I only found a response to conspecifics at a density of 300 larvae, although distance interacted with larval density and may have countered the effect of competition. Additionally, there seemed to be an effect of density when it was confounded with tank size, but this effect was not linear as would be expected under the IFD. The densities chosen for these studies were based on those previously seen occurring in other experimental setups using tanks of the same size (Resetarits, *unpublished data*). By assigning densities both at and above those observed, I

expected to cross a density threshold whereby the costs of intraspecific competition would have outweighed the perceived benefits of ovipositing in a larger pond. Given that I did not find such a difference between the two densities used, a likely explanation for this is that both densities were above the threshold and treated the same.

Differences in larval density did not have a negative, linear effect on oviposition, and the effect of conspecific density remains an open question in understanding the basis for habitat selection by females. Research conducted in separate geographic locations has demonstrated that female response to habitat variation can vary between populations (Eason, Jr and Fauth 2001). Additionally, *H. chrysoscelis* larvae suffer higher rates of mortality due to larval density at the UMFS than other regions (Resetarits, *personal observation*). This evidence could suggest that effects of intraspecific competition can vary regionally within the same species.

Overall, this research provides several valuable insights for ecological monitoring and habitat management. The first insight is that all models attempting to assess habitat selection should account for the distance traveled to all habitat patches within a system. While the assumption that individuals are free is almost always violated in natural systems, models can be more robust to this violation if they account for distance in their predictions. Additionally, the results of this set of experiments show presence of conspecifics plays an important role in habitat selection, indicating that current conspecific density is an important parameter for both ecological models and habitat management plans. Finally, these results indicate that costs of intraspecific competition, at high enough conspecific densities within a patch, can outweigh perceived benefits from other habitat factors. As such, future ecological model should account for the interactive effect of intraspecific competition with other factors.

CHAPTER II: SPATIALLY EXPLICITY HABITAT SELECTION. TESTING CONTAGION AND THE IDEAL FREE DISTRIBUTION IN *CULEX* MOSQUITOES

Introduction

According to the Ideal Free Distribution, colonizing individuals should assess the quality of each habitat patch separate from all other patches, and then use the matrix of information available to select the best habitat patch (Fretwell and Lucas 1970). However, recent studies have indicated individuals may not perceive habitat patches as completely separate from one another (Resetarits and Binckley 2009, Stier and Osenberg 2010, Resetarits and Silberbush 2016, Trekels et al. 2017, Hamman et al. 2018, Trekels and Vanschoenwinkel 2018). The perception of one patch may affect the perceived quality, either positively or negatively, of neighboring patches in a phenomenon known as spatial contagion (Resetarits et al. 2005). For instance, the presence of a fish predator within a pool has been found to have a negative effect on the perceived quality of neighboring ponds, which is known as risk contagion (Resetarits and Silberbush 2016, Trekels and Vanschoenwinkel 2018). The reverse effect can also be true, so the presence of a low-quality patch, such as a pool containing fish, can result in nearby, higher-quality patches receiving a more colonizers compared to localities where no predators are present. This phenomenon is known as habitat compression and this may also occur when there are no alternative habitats available (Resetarits 2005, Pintar and Resetarits 2017). For example, coral reefs with no neighboring reefs can receive two to four times more colonizers than coral reefs of the same quality with adjacent reef habitat (Stier and Osenberg 2010). Alternative to risk contagion, high quality patches can increase colonization of nearby low-quality patches in cases of reward

contagion. As an example, frogflies (*Megaselia randi*) prefer to oviposit on frog clutches containing dead eggs. When an intact clutch with no dead eggs is near a damaged clutch, however, the intact clutch receives more colonizers than it would if it were near another intact clutch (Hughey et al. 2012). Cases of contagion, whether risk or reward, can negatively impact populations as contagion can create ecological traps (Resetarits et al. 2005). Ecological traps are defined as instances in which individuals select habitat patches with poor, or poorer, habitat quality (Gates and Gysel 1978, Delibes et al. 2001). Often times ecological traps occur because individuals are using habitat cues that are unreliable or are no longer accurate. Risk contagion can exacerbate habitat loss because factors decaying one habitat patch may create a negative perception of neighboring patches, which in turn makes them less likely to be colonized even if they are high-quality patches. In contrast, reward contagion creates an ecological trap where poor habitat is perceived as a more suitable habitat due to its relative proximity to a higher-quality habitat patch.

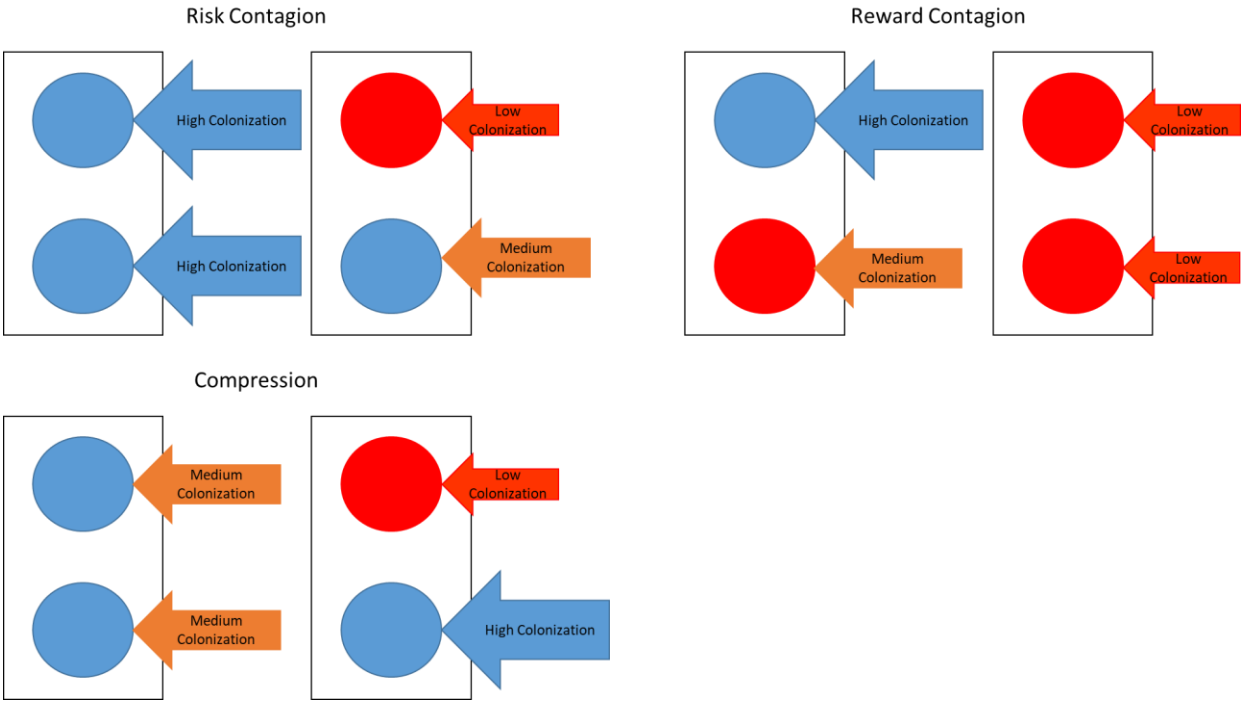

Figure 2.1. Examples of risk contagion, reward contagion, and compression. In cases of risk contagion, high quality pools (blue) near low quality pools (red) have lower rates of colonization than high-quality pools near other high-quality pools. In cases of reward contagion, low-quality pools near high-quality pools have higher rates of colonization than low-quality pools near other low-quality pools. When compression occurs, a high-quality patch near a low-quality patch receives more colonizers than a high-quality patch near other high-quality patches.

The effects of contagion and compression oppose the assumption of the IFD that individuals have perfect information about all patches. When contagion occurs, individuals within a population are misperceiving cues about habitat quality. However, the IFD second assumption that individuals are free to choose from all available habitat patches, is almost always violated in natural systems (Parker and Sutherland 1986). The question then becomes whether the IFD is robust to violations of its assumptions, and whether we can improve the model by compiling available information and parameterizing a theoretical model with real world, natural experiments. Treating contagion as a parameter for the IFD would mean adding spatial context as a predictor in the model and adjusting the expected response. Instead of simply predicting that

the quality of a patch will affect colonization, we now predict that the quality of neighboring patches will also have an effect. The IFD predicts that patches of the highest quality should receive the most colonizers. However, when including spatial context, high-quality patches that are near poor-quality patches can experience decreased colonization due to perceived risk (risk contagion), or colonization can increase if high quality patches are isolated or surrounded by low quality pools without an increase in perceived risk (habitat compression). At a larger spatial scale, we expect that the type and number of patches should affect the colonization of localities. More high-quality patches will drive up the rate of colonization of a locality, but colonization will only decrease significantly when all or most patches within a locality are low-quality (a form of regional contagion).

Finally, the IFD predicts that individuals should colonize the highest quality pools first. Based on the IFD, the addition of competitors to a high-quality patch should reduce perceived habitat quality by potential colonizers (refer to Fig. 1.1 in chapter 1). If contagion and compression effects are based on perceived quality then the addition of competitors, when patches are unequal in quality, should result in a decrease of compression and contagion effects due to a decrease in the difference of perceived quality.

To examine the interaction between the IFD and contagion, three outdoor mesocosm experiments were conducted testing oviposition habitat selection in mosquitoes (*Culex restuans*). The first experiment tested whether intraspecific competition affects habitat selection at the patch level by examining the response of *C. restuans* to pools containing conspecific larvae. Based on the predictions of the IFD, I expected conspecific density within a pool should negatively impact oviposition. The next experiment examined whether the presence of competition can cause a spatial contagion effect by arranging pools, both with and without larvae, into a more complex

spatial landscape. The expectation for this experiment was that the addition of larvae to a pool would negatively impact oviposition not only in that pool, but also in pools within the same locality. Additionally, I tested whether the presence of larvae free pools increased oviposition in larvae pools to determine whether there was a reward contagion effect. Finally, I tested how the effects of competition, as predicted by the IFD, interact with the potential contagion effect of resource availability to influence habitat selection. For this experiment, I predicted oviposition should be highest in pools with the most resources, as is predicted by the IFD. Additionally, I predicted, based on previous research, that resource availability should have a reward contagion effect (Pintar and Resetarits 2017). By adding conspecific larvae to the highest resource pools, I expected to drive oviposition towards lower resource pools and decrease any reward contagion effects.

Methods

Study Site

All experiments were conducted at the University of Mississippi Field Station (UMFS). The UMFS is a 318-hectare research complex located in Abbeville, MS. It is within the Eocene hills of the interior Gulf Coastal plain (Bohenek et al. 2017). There are over 200 ponds, as well a variety of streams, forests, fields and wetlands at the UMFS.

Study species

Culex restuans is an abundant mosquito species present at the UMFS and is an ideal species for oviposition habitat selection studies because females will readily lay eggs in experimental pools (Brust 1990). Previous studies have shown that over 98% of egg rafts collected from experimental pools at the UMFS are from *C. restuans* (Bohenek et al. 2017).

Additionally, a fair body of literature already exists outlining oviposition habitat preferences of *C. restuans*. Females avoid ovipositing in pools containing predators and conspecifics but prefer to oviposit in smaller pools with more resources (Reiskind and Wilson 2004, Chaves et al. 2009, Rubbo et al. 2011, Saward-Arav et al. 2016, Bohenek et al. 2017). *C. restuans* is also of particular interest to researchers because it is a vector of West Nile Virus (Sardelis et al. 2001). Because the habitat preferences of *C. restuans* are well documented and have been used to test previous contagion effects, *C. restuans* is an ideal species to study the interaction between spatial contagion and the IFD.

Experiment 1: Does Intraspecific competition affect habitat selection at the patch level?

The goal of this study was to map the response of ovipositing female *C. restuans* in response to conspecific larval density. This experiment began on 3 September 2017 and consisted of ten arrays, each made up of four pools (30L) situated 2.12 m from one other and surrounding a completely covered 70 L bait pool to attract mosquitoes to the area (Fig. 2.2). Treatments consisted of four conspecific density levels: 0 (control), 1.5 mL, 2.5 mL, and 3.5 mL, which corresponds to approximately 0, 330, 550, and 770 larvae in each pool. The experimental pools were filled with well water, 100 g. leaf litter as a nutrient base, and a randomly assigned treatment of *C. restuans* larvae. Because females avoid ovipositing in aged water, all arrays were deconstructed after 5 days.

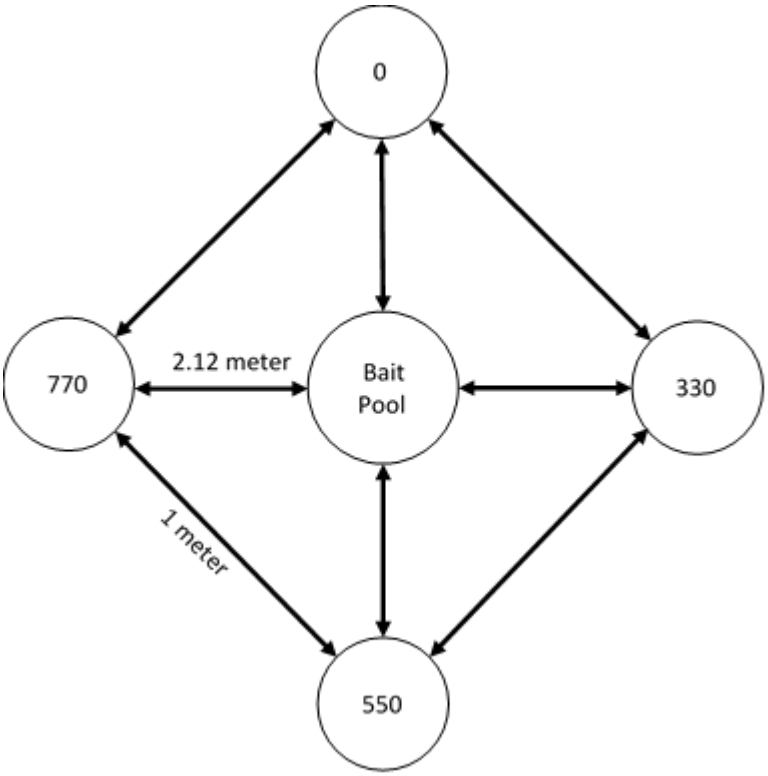

Figure 2.2. Competition evasion experimental design. Arrays consisted of four experimental pools and a bait pool. All experimental pools were 1 m from the bait pool and 2.12 from each adjacent experimental pool

Each pool was checked daily for egg rafts. Egg rafts were collected, counted, and then discarded. Egg rafts from this experiment were not collected to identify larvae to species, but previous research has shown that > 98% of all egg rafts collected in experimental pool at UMFS are *C. restuans* (Bohenek et al. 2017). This experiment was concluded on 29 September 2017. Analysis for this experiment was conducted using a linear mixed-effects model with density as the main effect and the mean number of eggs rafts as the response, using block as a random factor. Additionally, a one-tailed Dunnett's test was used to compare all experimental groups to the control. Analysis was done in R v.3.5.2 using the multcomp and models were constructed and analyzed using the lme4 and lmerTest packages (Hothorn et al. 2008, Bates et al. 2015, Kuznetsova et al. 2017).

Experiment 2: Does the presence of conspecifics cause a contagion effect?

This experiment tested whether the presence of conspecifics within a patch can have a risk contagion effect. A 4×2 factorial design was established on 6 October 2017, consisting of seven blocks each containing 12, 30 L pools. All pools were filled with ground water and 100 mg of leaf litter. Additionally, half of the pools in each block contained 3.5 mL of *C. restuans* larvae, while the other half served as larvae free controls. Pools were arranged into four groups, hereafter referred to as locality types: all control (CCC); 2 control, 1 larval treatment (CCL); 1 control, 2 larval (CLL); and all larval treatment (LLL) (Fig. 2.3). Blocks were kept up for 14–15 days, except for block one which was taken down after five days. Pools were checked daily for egg rafts and any egg rafts were counted and removed. This experiment ended on 28 October 2017.

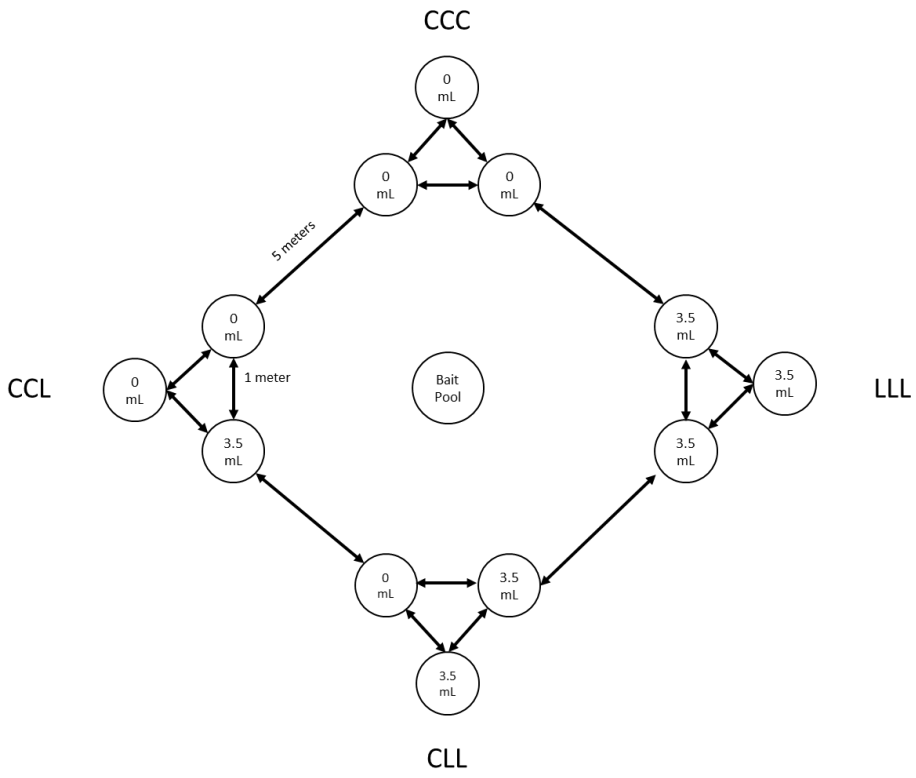

Figure 2.3. Schematic for experiment 2. For each block, 12 pools were separated in to four localities and two pool types. Pools either contained no larvae (0 mL) or 770 larvae (3.5 mL). Localities varied in the number of each pool type.

To test the effect of intraspecific competition on habitat selection, a t-test was conducted comparing the number of egg rafts deposited in control and competition pools, using a log transformation. Then, a linear mixed-effects model compared the rate of oviposition with locality type as the predictor, the log transformed number of egg rafts per locality as the response, and block as a random factor. This model used Type III analysis with Satterhwaite's method (Bates et al. 2015). Additionally, pairwise comparisons were conducted using Tukey's Post Hoc test for comparisons. Because two of the locality types only contained one pool type it was impossible to do a full 4×2 factorial analysis. Instead, all data was split in to two subsets: one for control pools and one for larval pools. The data for the control pools was normally distributed, but the number

of egg rafts in larval pools was log transformed. Then, linear mixed-effects models were constructed for each subset, with locality type as the predictor variable and mean number of eggs rafts as the response, treating block as a random factor. Tukey's Post Hoc test was then conducted on each model comparing pools from each locality type. Analysis used R v.3.5.2 and the packages lme4, lmerTest, and multcomp were used for model construction and analysis (Hothorn et al. 2008, Bates et al. 2015, R Core Team 2019).

Experiment 3: Density Modified Contagion Effects

The purpose of this experiment was to test the interaction between spatial contagion and the ideal free distribution. This was an outdoor experiment set up using a 2×3×2 factorial design. The first block was established on 12 September 2019. Eight blocks were set up using a tiered design: twelve pools in each block divided in to two different region types, three different locality types, and two different pool types (Fig 2.4). All pools were filled with ground water and had either 0.5 kg leaf litter added (high leaf litter pools) or 0.1 kg of leaf litter (low leaf litter pools). The two regions within each block were distinguished by conspecific larvae; one region had no larvae present and the other block had 3 mL of larvae added to each high leaf litter pool. Additionally, within each region pools were grouped into localities. Each locality contained 2 pools; localities consisted of two high leaf litter pools (homogenous high), one high leaf litter pool and one low leaf litter pool (mixed), or two low leaf litter pools (homogenous low). Within each locality pools were placed 1.5 m apart. Localities were placed 5 m away from adjacent localities within a block. All plots were separated by a minimum of 40 m. Each block was taken down after seven days, as oviposition drops precipitously as pools age (Bohenek and Silberbush *personal observation*).

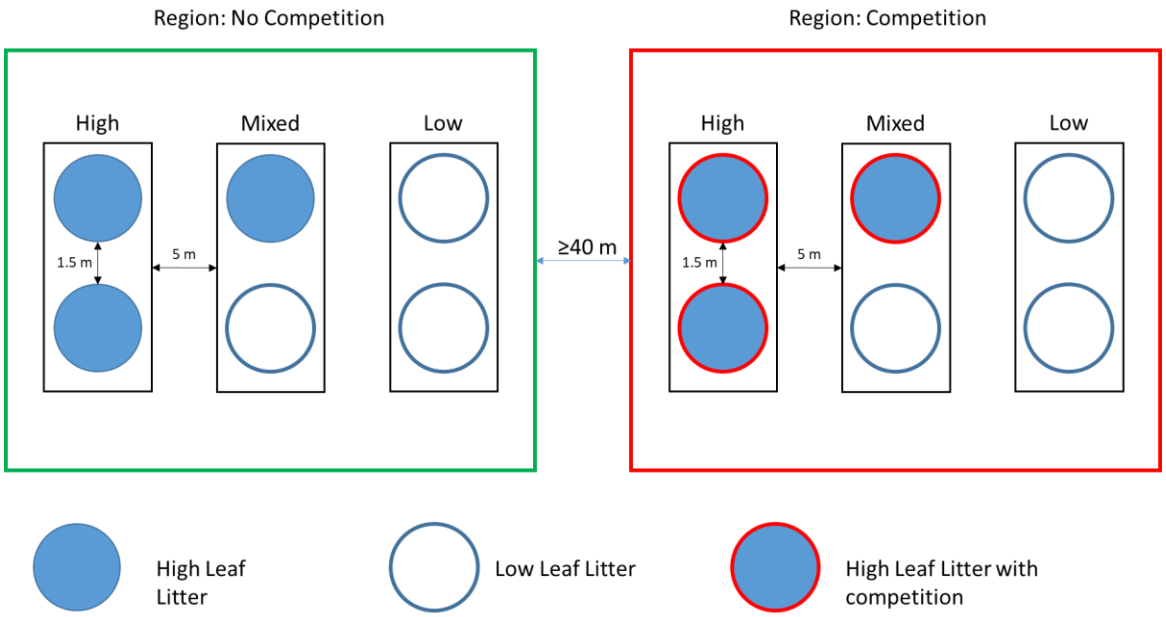

Figure 2.4. Schematic for Experiment on Density Modified Contagion. Experiment consisted of regions with (green) or without (red) *C. restuans* larvae. Pools were either High Leaf Litter (0.5 kg) or Low Leaf Litter (0.1 kg). Pools were separated into localities of all high pools, mixed, or all low.

After blocks were set up, they were checked daily for egg rafts. Any egg rafts found were counted, collected, and reared for future blocks in this experiment. The experiment was terminated on 13th October 2019.

For patch level analysis, I created a linear mixed-effects model using the mean number of eggs deposited as the response, patch type as a predictor, and block as a random factor. Patch type for the purpose of this model was based on nutrient level, locality type, and the regional presence of conspecifics. As such, there were eight different patch types, which are outlined in Table 2.1. Once the model was constructed, I compared the 8 different patch types using a series of seven contrasts based on *a priori* hypotheses. The seven contrasts used are described in Table 2.2. Combined, these contrasts addressed the following questions: 1.) Does nutrient availability

affect oviposition? 2.) Does competition interact with nutrient availability? 3.) does resource availability have any contagion or compression effects? 4.) Does competition interact with any contagion or compression effects caused by resource availability.

Table 2.1. Summary of the different patch types used for analysis. Patch type was assigned based on nutrient level, locality type, and presence/absence of conspecific larvae at the regional scale. Patches could be either high (0.5 kg) or low (0.1 kg) nutrients. All patches were within high, mixed, or low localities. Conspecific larvae were either present or absent at the regional level.

Patch Type	Nutrient Level	Locality Type	Conspecific Presence/Absence
HHN	High	High	No
HHY	High	High	Yes
HMN	High	Mixed	No
HMY	High	Mixed	Yes
LLN	Low	Low	No
LLY	Low	Low	Yes
LMN	Low	Mixed	No
LMY	Low	Mixed	Yes

Table 2.2. Outline of the seven non-orthogonal contrasts used for analysis at the patch level. Contrasts were used to determine effects of resource availability, competition, and resource:competition interactions.

	Hypothesis	HHN	HHY	HMN	HMY	LLN	LLY	LMN	LMY
Contrast 1	Are high and low patches different?	1	1	1	1	-1	-1	-1	-1
Contrast 2	High Nutrient x competition interaction.	1	-1	1	-1	0	0	0	0
Contrast 3	Low Nutrient x competition interaction.	0	0	0	0	1	-1	1	-1
Contrast 4	Are high patches different in mixed localities?	1	1	-1	-1	0	0	0	0
Contrast 5	Are low patches different in mixed localities?	0	0	0	0	-1	-1	1	1
Contrast 6	Does competition effect risk contagion?	1	-1	-1	1	0	0	0	0
Contrast 7	Does competition effect reward contagion?	0	0	0	0	1	-1	-1	1

In addition to patch-level tests for spatial effects, I constructed a two factorial linear mixed model of oviposition at the locality level. For this model, the mean number of egg rafts per locality was the response variable, locality type and conspecific presence/absence within the region were predictors, and block was used as a random effect. Both linear mixed models in this

experiment were constructed using the lme4 package (Bates et al. 2015). Contrasts were set up and conducted using the multcomp package (Hothorn et al. 2008).

Rearing and quantifying larvae

Egg rafts were collected prior to the beginning of each experiment and were reared in 100 L wading pools until they reached the fourth instar larval stage. Because an individual egg raft from *C. restuans* can contain 200-1000 individual eggs, larvae were quantified by volume, with 0.5 mL of larvae being equivalent to approximately 110 individuals.

Results

Experiment 1

From 3 – 29 September 2017 a total of 3,099 egg rafts were collected from 10 arrays. There was a significant effect of density on the rate of oviposition ($F_{3,27} = 6.14$, $P = 0.002$); there were significantly more egg rafts laid in the 0 larvae treatment than the 330 ($Z = -2.711$, $P = 0.009$), 550 ($Z = -3.570$, $P < 0.001$), or 770 ($Z = -3.834$, $P < 0.001$) larvae treatments (Fig. 2.5).

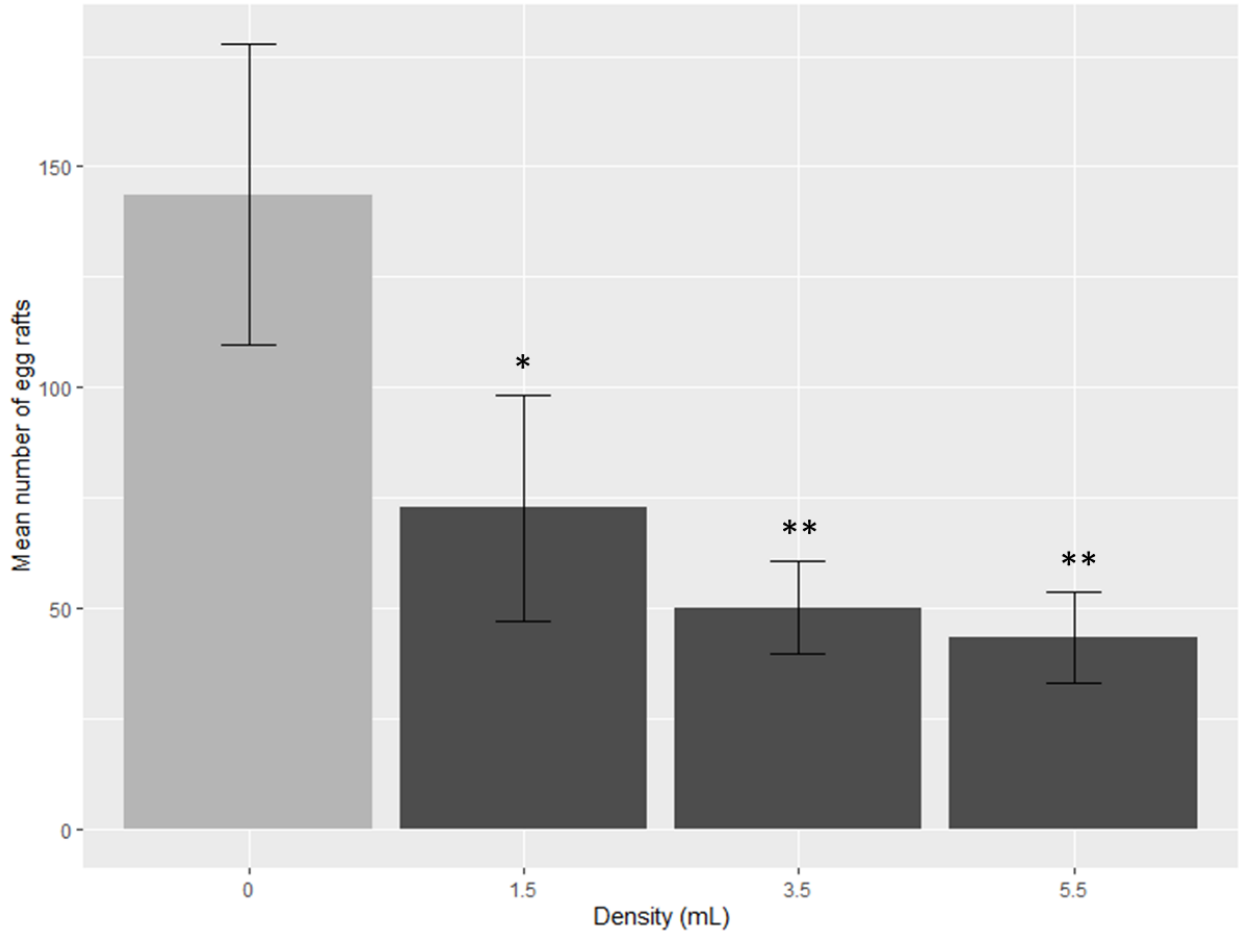

Figure 2.5. Effects of conspecific larval density on oviposition by *C. restuans*. There was a significant difference between pool containing 0 larvae and pools containing 330, 550, or 770 larvae. Significant values ($P < 0.05$) are indicated by asterisk. Highly significant values ($P < 0.001$) are indicated by two asterisk.

Experiment 2

For this experiment, 3,143 egg rafts were collected over 22 days. A t-test of the two pool types (larvae free vs. larvae pools) again showed a significant effect of conspecific larvae on the number of egg rafts laid ($T = -6.89$, $P < 0.001$, $DF = 50.44$, Fig 2.6). A linear mixed-effects model comparing locality type showed a significant difference between locality types based on

conspecific larvae ($F_{3,15}$ = 10.702, P = 0.005, Fig 2.7). A Tukey post hoc test for comparisons showed a significant difference between the locality containing entirely control pools (CCC) and the locality containing entirely larval pools (LLL) (Z = -5.264, P < 0.001) as well as the 1 control 2 larval pools locality (CLL) (Z = -2.711, P = 0.03). There was also a significant difference between localities containing 2 control pools and one larval pool (CCL) and the all larval pool localities (LLL) (Z = -4.316, P < 0.001). Finally, there was a marginal difference between the CLL and LLL localities (Z = -2.553, P = 0.052). All comparisons are summarized in Table 2.1 and visualized in Figure 2.7.

A linear mixed-effects model of control pools showed no significant effect of locality type on the number of egg rafts laid ($F_{2,28}$ = 0.35, P = 0.70, Fig 2.7a). Additionally, a linear mixed-effects model of larval pools showed no significant effect of locality type on oviposition ($F_{2,28}$ = 2.04, P = 0.14, Fig 2.8b).

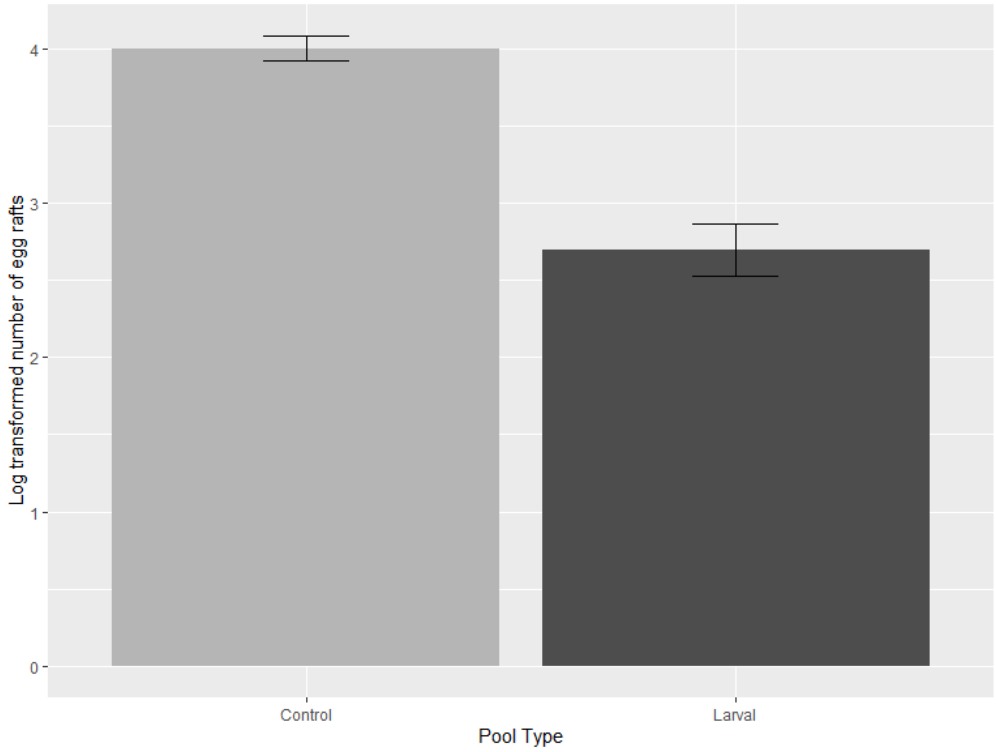

Figure 2.6. The effect of larvae on oviposition within a complex spatial landscape. Females showed a clear preference for pools without larvae.

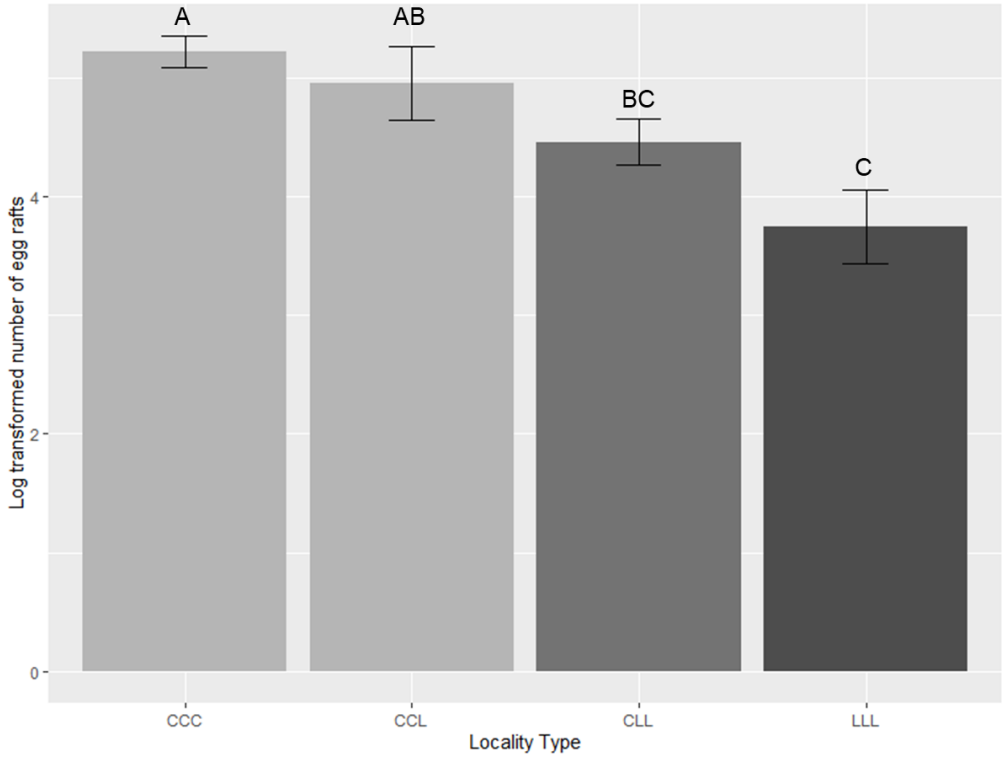

Figure 2.7. The effect of larvae on oviposition at the locality level. The different locality types: 3 control pools (CCC); 2 control, 1 larvae (CCL);1 control, 2 larvae (CLL); and all larvae (LLL). Linear mixed-effects model showed a significant effect of locality type, with differences indicated by letter grouping. Pairwise comparisons were made using a Tukey Post Hoc test for comparisons.

Table 2.3 Comparison of locality types using a Tukey Post Hoc Test. Summary includes difference between mean of locality types, upper and lower limits of confidence intervals, and p value. Significant differences are indicated in bold, marginal values are in italics.

Comparison	Estimate	Standard Error	Z-value	P-value
CCL-CCC	-0.2661	0.2808	-0.947	0.7792
CLL-CCC	-0.7613	0.2808	-2.711	**0.0337**
LLL-CCC	-1.4783	0.2808	-5.264	**<0.001**
CLL-CCL	-0.4953	0.2808	-1.764	0.291
LLL-CCL	-1.2122	0.2808	-4.316	**<0.001**
LLL-CLL	-0.717	0.2808	-2.553	*0.0523*

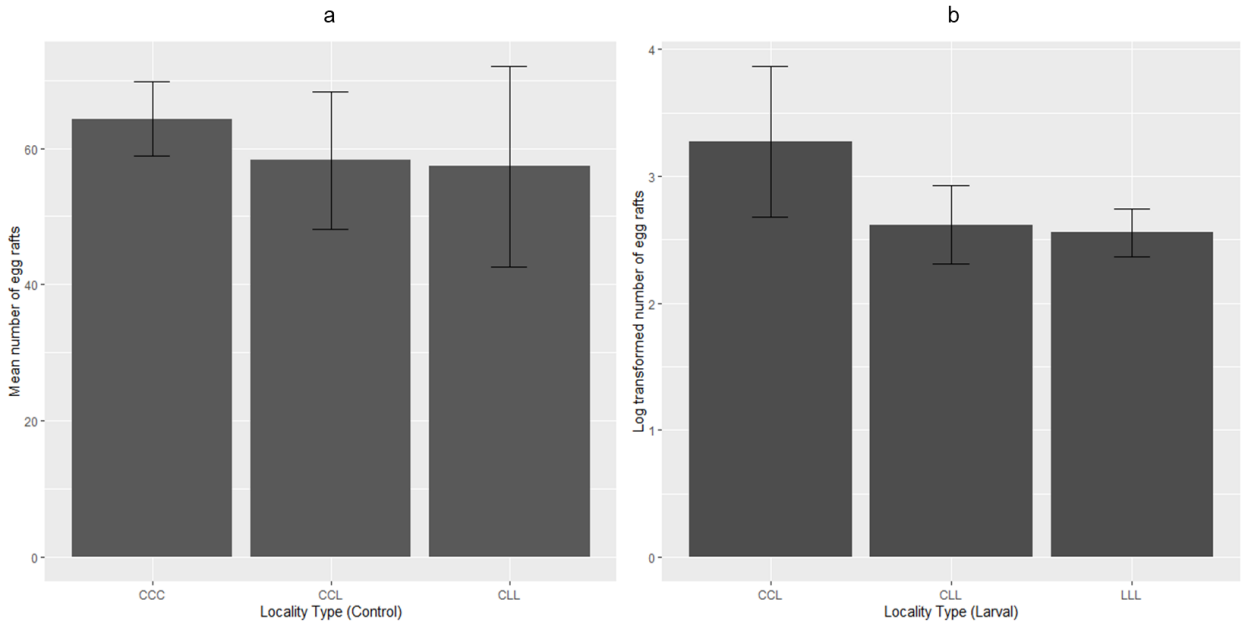

Figure 2.8. (a) The number of egg rafts laid in control pools based on locality type. There was no significant difference between control pools from different localities. (b) The number of egg rafts laid in larval pools based on locality type. There was a marginal difference in the number of eggs rafts laid in the CCL locality versus the CLL locality ($p = 0.099$) and the LLL locality ($p = 0.065$).

Experiment 3

I collected 36,034 egg rafts from 96 pools over the course of 30 days. High resource patches received significantly more egg rafts than low resource patches (Contrast 1, $z = 8.496$, $df = 1$, $p < 0.001$). However, none of the other contrasts tested yielded significant results. The results of all contrasts are outlined in Table 2.3. Oviposition in each of the eight pool types is visualized in Figure 2.9.

At the locality level a linear mixed effects model showed a clear effect of locality type on the rate of oviposition ($F = 10.64$, $p < 0.001$, $df = 2$). The presence of larvae within the region had no effect ($F = 2.74$, $p = 0.10$, $df = 1$) and there was no interaction between locality type and presence of larvae ($F = 0.59$, $p = 0.559$, $df = 2$) (Fig. 2.10).

Table 2.4 A summary of all contrasts conducted on the model to determine effects of nutrient availability and competition, and to test for contagion/compression effects. Significant effects are in bold.

	Hypothesis	z-value	df	p-value
Contrast 1	Are high and low patches different?	8.496	1	**< 0.001**
Contrast 2	High Nutrient x competition interaction.	1.083	1	0.890
Contrast 3	Low Nutrient x competition interaction.	0.765	1	0.982
Contrast 4	Are high patches different in mixed localities?	-0.781	1	0.979
Contrast 5	Are low patches different in mixed localities?	0.286	1	1.00
Contrast 6	Does competition effect risk contagion?	-0.550	1	0.997
Contrast 7	Does competition effect reward contagion?	-0.557	1	0.997

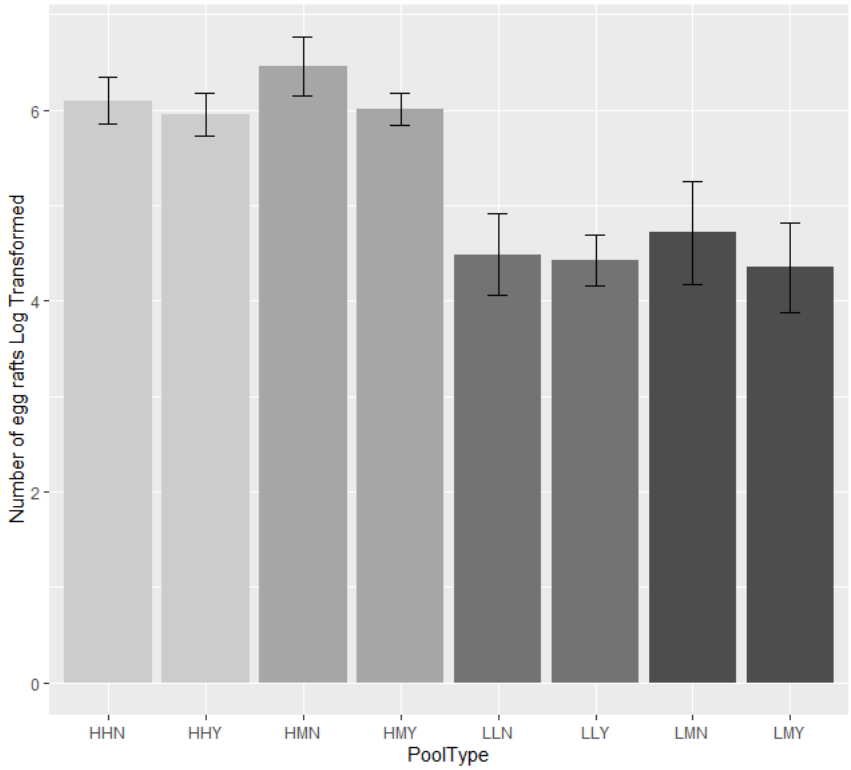

Figure 2.9. Rate of oviposition by *C. restuans* in each of the eight pool types.

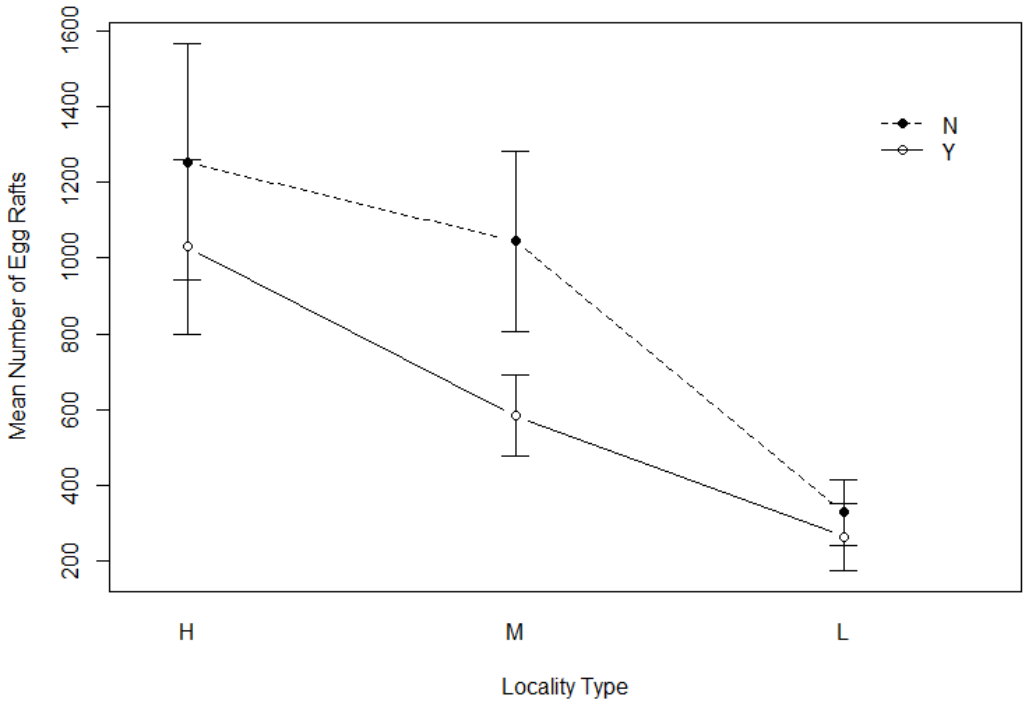

Figure 2.10. Differences Between localities when larvae are absent (N) and present (Y). There was a strong effect of locality type on oviposition (mean number of egg rafts). There was no effect of larvae, *and there* was no interaction between locality type and larvae.

Discussion

The results of this series of experiments show that larval competition plays a complex role in oviposition habitat selection by *C. restuans*. My initial experiment showed a clear effect of larval presence on oviposition preference at the patch level and this was confirmed in testing a more complex spatial structure. That competition did not affect oviposition in the final experiment suggests that when nutrient availability is high competition becomes a negligible factor in selecting a habitat patch.

Contrary to what was expected, there was no evidence for a risk contagion effect of larvae on nearby high-quality pools. When the spatial landscape was more complex, with more

patches being divided into locality types, the locality type of a pool did not influence oviposition in that pool. Females still showed a strong preference for patches not containing conspecifics, but that effect did not bleed into neighboring patches, nor did patches containing conspecifics create a perceived risk in conspecific free patches. Additionally, I did not find any evidence for a locality level contagion effect, as oviposition rates based on locality followed a more linear trend than would be expected if contagion were occurring. Overall, females were able to accurately assess habitat quality based on conspecific density even when the landscape was spatially complex, consistent with the predictions of the IFD.

The final experiment adds to the complexity of habitat selection by examining not only the effect of competition, but how competition interacts with resource availability at various scales. At the patch level this experiment showed no effect of larval conspecifics on oviposition habitat selection. There was a clear effect of resource availability, as females had a strong preference for patches where nutrient availability was high. The locality type a pool was in did not affect oviposition rates, indicating that there were no spatial effects. At the locality level I found that locality type significantly impacted rate of oviposition with the homogenous high locality receiving the most oviposition and the homogenous low locality receiving the least. The effect of nutrient availability at the locality level was not diminished by the presence of conspecific larvae, again indicating that competition did not affect oviposition rates in this experiment.

Testing for contagion effects while also examining the effects of competition could improve our understanding of the decision making algorithms responsible for habitat selection. Certain environmental factors within habitats may be prioritized over others. For example, in temporary freshwater ecosystems, it is often the case that predation is of highest importance,

followed by other factors such as shade, resource availability, and pool size (Bohenek et al. 2017, Pintar et al. 2018). Competition is thought to be of relatively low importance compared to resource availability, since competition is thought to be largely a result of limited resources (Scott 1990). The fact that conspecific larvae did not have a significant effect on oviposition in the final experiment while there was a strong effect of larvae in the first two experiments indicates that the effects of competition on oviposition are negligible when resource availability is high, and therefore resource competition is low. However, this set of experiments only tested the effects of competition at the larval stage, and as such these results can only be interpreted for competition at the larval stage. *C. restuans* has multiple life stages and ovipositing females may be assessing patches for the presence of competitors at varying stages, such as other adult females, while these experiments only assessed the effect of one life stage.

One of the main consequences of high conspecific density is increased competition for resources (Wilbur and Collins 1973). If habitat selection is based on potential fitness then the results of this set of experiments support Wilbur and Collin's theory, as competition had a more important role in habitat selection when resources were lower. However, conspecific competitors can also effect life history through direct chemical cues (Bohenek and Resetarits 2018). Additionally, research on mole salamanders (*Ambystoma talpoideum*) has shown that the effect of competition on larval growth is independent of the effects of resource availability (Semlitsch 1987). Other ecological factors, such as predation and resource availability, affect habitat selection due to potential impacts on fitness. However, predation is the only factor that consistently causes spatial effects (Resetarits and Binckley 2009, Resetarits and Silberbush 2016, Trekels and Vanschoenwinkel 2018). Further research should continue to explore how spatial

dynamics relate to model predictions and the underlying mechanisms causing neighboring patches to affect perceived habitat quality of other patches.

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Biological Graduate Students' Journal Club
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